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Introduction

Space exploration offers an unprecedented opportunity to study the evolution of bipedalism, the use of two feet as the primary method of locomotion. Among mammals, this adaptation is uniquely human (Wilson:52). Bipedalism is impossible in the weightlessness of space, and astronauts have had to adapt other means of locomotion. A better understanding of human adaptation to weightlessness may offer insight to the human evolution of bipedalism.

Bipedalism and weightlessness have resulted in physical as well as behavioral changes. In bipedalism, the weight of the body shifted from four to two legs and feet, transmitting the load vertically through the spinal column. Evolutionary changes occurred in the legs, knees, pelvis, feet, and spine. Weightlessness unloads these weight-bearing bones and astronauts have been observed to experience bone mass loss after exposure to weightlessness. This paper will examine human adaptation to space for indications of hominid evolution to bipedalism.

Evolution of Bipedalism

Bipedalism is arguably the oldest human behavior, predating others by at least one million years. Other uniquely human behaviors such as language, tool-making, or abstract reasoning require the parieto-occipital or association region of the brain, located within the frontal lobes (Laughlin:52, Falk:66). Endocasts of fossil hominid skulls are interpreted as showing that frontal lobe evolution started with *Homo habilis* approximately two million years ago (Falk:50). The oldest conclusive evidence of hominid bipedalism is fossil remains of footprints in southeast Africa attributed to *Australopithecus afarensis*, one predecessor of *Homo sapiens*, that are approximately 3.6 million (Leakey:103). Therefore, understanding hominid adaptation to bipedalism is essential to comprehending the origins of human evolution.

Evolution is the theory that the frequency of genetically determined characteristics changes within a population over time. The mechanism for evolution is the range of variability for a genetic trait, random mutations in the genctic material, and natural selection. If a genetic variation or mutation offers an advantage in survival or reproduction, the individuals with that characteristic are apt to produce more offspring and it is passed on through reproduction. Eventually, this natural selection increases the percentage of the population with that genetic advantage (Wilson:75-76,80; Leakey:356).

Individuals cannot evolve. Genetic composition is determined at the conception of an individual and does not change during its lifetime. But because of natural selection, the ability of an individual to adapt to a changing environment is an evolutionary factor. Individuals of species that are flexible in their habitats, and that adapt to habitats that make it easy to disperse, have an advantage over individuals of species that cannot adapt. The survival of a species depends on the survival of individuals of that species (Wilson:91-92).

For primates, locomotion to obtain food is essential for survival. All primates use their hindlimbs in locomotion and while at rest to support the weight of their body. This is reflected in the bone structure of the hindlimbs, which shows similarities in the organization and comparative proportional measurements of functional bone groups (Napier:386). But while primate hindlimbs show similarity, there are variations which reflect evolutions to different primary modes of locomotion. This indicates two possibilities about primates; they have a shared past with a common ancestor, and they are highly adaptive.

The common ancestor was likely a small, arboreal quadruped whose means of locomotion was climbing, running, scampering, and leaping along and among the tree limbs (Jolly:137). Primitive primates evolved the ability to grasp with all four limbs using opposable thumbs and toes, a significant skeletal evolution for arboreal life (Cartmill:46; Napier:387,390). Primates have subsequently evolved such specialized primary locomotions as climbing, hopping, arboreal and terrestrial quadrapedalism, brachiation, and knuckle-walking. But many primates adapt a variety of locomotions; terrestrial quadrupeds climb trees, knuckle-walkers lapse into bipedalism, and brachiators scamper on the ground. The significant behavioral adaptation for apes and old world monkeys, the primates most closely related to humans, is flexibility in locomotion.

While not conclusive, evidence suggests that *H. sapiens* evolved from tree-climbers. Fossil examination of *A. afarensis* reveals long, hooked phalanges on hands and feet, short hindlimbs, funnel-shaped thorax, large pisiform, and a cranially oriented shoulder joint, which are all selections for tree climbing (Leakey:195). The modern human wrist also bears evidence of selection for suspended loads (Lewis:167-8). Although *H. sapiens* is uniquely bipedal, its adaptation to bipedalism is revealed in the evolution of its skeleton.

Adaptation is a result of competition or expansion for survival in different econiches (Wilson:95). Most theories of hominid evolution to bipedalism focus on freeing the hand for various purposes such as food-gathering, tool-making, and/or infant care, although some imaginative theories regarding sexual display and thermal protection have been proposed (Falk:89-97). But the free hand theories ignore chronology and referential models. Hominid tool use and altricial infants are characteristics associated with larger brains which occurred at least one million years after bipedalism. Other primates manage to gather food, carry infants, and even use rudimentary tools without the "free hands" associated with bipedalism.

Striding is more efficient than knuckle-walking over long distances, therefore, the natural selection advantage offered by bipedalism is efficiency in movement (Leakey:91). Consider bipedalism as an adaptation for survival in a changing environment where food was increasingly sparse and widely scattered (Leakey:91; Falk:97). In theory, a cooler or drier climate resulted in less vegetation which decreased the available food. *Homo's* semi-arboreal primate ancestor may have had to cross stretches of barren savannah in order to gather enough food to survive. Given this assumption, three important considerations are posed. The first is the error in discussing free hands, since opposable thumbs and toes are a widely used characteristic of primates (Richards:143-150). Leaving the safety of the trees to face predators and compete with scavengers for food may have been a desperate act that eventually resulted in the sacrificial evolution of the grasping abilities of the feet (Messman:55). Second, the eventual spread of hominids can be considered in terms of adaptation to an environment. The grassy savannah is an excellent habitat for long-term dispersal (Wilson:91). Efficient locomotion and adaptation to the grassy savannah appear to be a fortunate combination, and can be one reason that hominids eventually fanned out over the Earth. Third, survival of hominids required taking risks and venturing into unknown territories. It is assumed that during the climate change that drove our ancestors to bipedalism, other primitive primates remained in the relative security of the trees. These primitive primates maintained the status quo, survived, and have not evolved significantly in comparison to the apes (Jolly:125). But other species did not adapt, or took unfortunate risks, and did not survive. Ancestors of humans and apes took risks, survived, adapted, and evolved. While this correlation does not prove causal linkage, this could be interpreted to indicate that we are genetically inclined to be risk-takers and adventurers.

Physiological Adaptation for Bipedalism

Forces applied to a body because of behavioral adaptation result in physical adaptation, and the study of force on the structure of a living body is biomechanics (Badoux:1,3). Bone is a living tissue that is constantly being replaced; its growth is very susceptible to the application of force. Wolff's law states (in summary) that usage affects bone to change its internal structure, form, and function (Jacob:88). The stress and strain applied to bones, and the resulting change to the bone is an appropriate application of biomechanics.

The skeleton's functions include serving as the body structure to counter the affects of gravity, and as an anchor for muscle attachment. Therefore the two major forces that act on skeletal bone growth are muscle strength and environmental factors, which includes gravity. Much muscle tension on bone is related to gravity. Quadrupeds must hold the weight of the body above the ground using their legs, and this load is transmitted primarily along the spine. The spine alternates vertebrae and discs for flexibility and movement, and is stiffened by muscle action (Badoux:1-12). A change of gravitational force, either in direction (as in adaptation to bipedalism) or magnitude (as in adaptation to weightlessness) will affect the muscle force used to counter gravity, and subsequently the force transmitted to the bone. The legs, spine, and pelvis are most affected by gravity in bipedalism, so changing gravitational force can be expected to have the greatest affect on these bones.

In addition to the inherent force transmitted to the skeleton to counter gravity, muscles contract to move a body part, and this contraction transmits force to the bone. Walking uses muscles that apply the greatest force to the bipedal skeleton (Gregor:197). Bipedal striding can be expected to affect the bones in the legs and spine because of the associated work of these muscles. This naturally affects bone growth, resulting in biological adaptation as increased mineral deposits over time. (Ariel:27-29). In addition to the inherent muscle force applied to the lower skeleton as a result of countering gravity, a change of gravity can compound the changing force applied to the skeleton as a result of changing muscle use.

Bone is a homeostatic system involving mineral deposit and resorption. Three to five percent of an adult skeleton is actively undergoing change and remodeling at any time (Strand:479). For example, the distal portion of the femur is replaced approximately three times a year (Tortora:101). Approximately 30% of the bone matrix is a three-dimensional trusswork of organic protein-polysaccharides which give the bone tensile strength. Osteoblast cells in the blood secrete the material that forms organic bone tissue. The remaining 70% is inorganic hydroxyapatites which give the bone its compression strength. Hydroxyapatites are formed from calcium and phosphate in the hlood which adheres to the organic trusswork (Strand:478-487; Jacob:83-88; Tortora:93-102; Hole:140-144).

Besides serving as a structure, the skeleton serves as a reserve for the calcium needed for muscle activity. Bone demineralization is also necessary to prevent excessive bone growth and to remove dead osseous tissue, and occurs as a result of osteoclast cell action. Osteoclast cells are also carried by blood, and contain enzymes that break apart the hydroxyapatite matrix to release calcium for resorption by the blood or renal elimination.

The homeostatic system of bone growth and demineralization is an extremely complex system regulated by many factors that are still not fully understood. However, enough evidence exists to focus on the role of the thyroid and parathyroid glands in monitoring calcium blood serum level. Calcium is absorbed from food in the small intestines. A calcium deficiency is sensed by the parathyroid which increases secretion of parathorome (PTH) to increase osteoclast bone demineralization activity. Simultaneously, PTH stimulates the kidneys to increase secretion of a hormonal form of vitamin D_3 ($1,25\text{-}(OH)_2\text{-}D_3$) that acts on the intestines to increase calcium absorption.

An excess of calcium is sensed by the thyroid which excites secretion of two hormones. Calcitonin decreases blood calcium by inhibiting osteoclast activity and bone resorption. Thyroxine enables growth hormone (GH) production in the pituitary glands. The liver produces somatomedian in response to GH which stimulates cartilage cell production for bone formation. Excess calcium is also sensed by the parathyroid which decreases PTH secretion to reduce osteoclast activity in the bones. A PTH decrease reduces the hormonal D_3 released by the kidneys to decrease calcium absorption in the small intestines, and the calcium content of feces is increased. A PTH reduction also increases renal elimination of calcium (Vander:346-349,407; Strand:483-487; Jacob:513-528; Holick:166).

Osteoblast production and mineral deposition is also regulated by the application of force. A greater applied force results in greater bone deposit (Strand:480, Jacob:84). Physical training and bone injuries stimulate bone production (Van Huss:27). While there is no certainty on the mechanics of osteoblast production as a result of bone loading, one theory involves electrical stimulation. Similar to the piezoelectric effect, the mechanical loading is theorized to generate an electrical charge whicb stimulates bone growth (Strand:480).

Usage causes bone adaptation, and human adaptation to bipedalism resulted in natural selection on these favored adapted factors. This has effected the evolution of the human skeleton. The scapula of *H. sapien* is relatively broad reflecting its tree-climbing origins, but is best adapted to provide stability while lifting (Roberts:198; Badoux:17). The spine is the major weight-bearing bone assembly in the human body. It has adapted secondary curves in order to support the weight of the head, shoulders, and forelimbs. These secondary curves are not present at birth but develop with time and the affect of gravity (Badoux:16-17). The knee has evolved many adaptations including the ability to lock when extending the leg, providing stability when striding (Tardieu:72). The big toe has aligned with the other toes, and the feet have evolved arehes for stability (Messman:56, 59). All of these skeletal adaptations offer greater efficiency, and natural selection advantage, for human bipedalism.

Behavioral Changes for Weightlessness

Because of the duration of the missions and the volume of space available for locomotion, observations from the three Skylab missions in 1973-1974 offer unusual insight into human behavioral changes to weightlessness.

Locomotion in three dimensions in weightlessness is somewhat analogous to motion underwater except that water offers resistance. Newtonian physics explains why stopping or slowing down in space is very difficult. Astronauts can swivel around their center of mass, but can not change direction by waving or flailing their arms or legs. Acrobatic type motion is often incorporated. Transversing a weightless volume is accomplished by pushing against a fixed surface with a low force resulting in drifting, described as "if underwater" and "dreamlike, disembodied" (Cooper:7, 73-78). A greater force results in becoming human projectiles, which was used on Skylab only in the large volume of the upper deck since safety was a major concern.

Locomotion in weightlessness is often accomplished by using the arms for movement along a surface (Van Huss:26). Hand-holds were found to be important for leverage in Skylab, and test equipment was used as latching points (Cooper:75). In this sense, locomotion in weightlessness resembles arboreal brachiation. Attempting to use the legs as in bipedal striding had the effect of pushing away from a surface instead of along it, unless the arms were used to push against an upper fixed surface (*Ibid*:22). The legs were useful for anchorage either by wrapping them around a latch point or by using special cleated shoes that locked into grid panels in the floors (*Ibid*:15, 90-91). Stability while working was important to the astronauts in order to avoid drifting off, and to be able to apply force on an object without causing motion in themselves. They found that they had to jam and wedge themselves against stationary objects, and apply muscle tension in different ways than they used on Earth.

Adaptation to locomotion in space took a few days. The astronauts had to learn how to avoid crashing into things or stranding themselves away from leverage points (*Ibid*:36, 79). The tendency to drift away from work activities and having objects drift away while working was somewhat irritating (*Ibid*:90, 92). Most Skylab participants preferred a strong local vertical, with workspace arranged along gravity-based axes with definite floors and ceilings instead of being arranged for maximum use of space. Most found it slightly unsettling for themselves or others to be out of kilter with the local vertical (*Ibid*:23-24, 70, 109-111).

Not all explorers totally enjoyed weightlessness, and some adapted better than others. Antidotal accounts of Skylab 4 Pilot William Pogue report that he "suffered the most from weightlessness," "had the greatest trouble adjusting to new verticals," and "felt he was the clumsiest of all Skylab astronauts" (*Ibid*:75-78,92, 109). On the other hand, Skylab 4 Science Pilot Edward Gibson is reported as "the best adapted to life in space-at least he was the most able to break away from the patterns of life on earth" (*Ibid*:111). He was the only participant to unequivocally recommend zero-gravity for future space stations (*Ibid*:93). The remaining seven participants seem to range somewhere between these data points. This provides some information on the variability of human behavioral adaptability.

But in general, all the astronauts genuinely enjoyed the sensation of weightlessness. Especially initially, it was exhilarating to perform intricate acrobatics with little effort and the crews readily explored their expanded abilities (*Ibid*:36,73-78). Flips were incorporated into routine motion simply for pleasure; Skylab 2 Commander Pete Conrad "never got tired of weightlessness" and games involving abilities unique to weightlessness quickly developed (*Ibid*:174). Locomotion in weightlessness was found to be both efficient and pleasurable. Static suspension in space was also found to be a generally positive experience. The body assumes a natural slight crouch in weightlessness with arms chest high and elbows and knees bent that has been described as "resembling a quadruped" (quote:Van Huss:19; also: Nicogossian:136-137; Thornton:330-336; Cooper:116). Skylab 3 Science Pilot Owen Garriott described drifting and floating in space as "pleasant" and "not uncomfortable" (*Ibid*:22). Most of the Skylab participants recommended large open space in future space stations to enjoy weightlessness (*Ibid*:78). Most of the nine Skylab participants agreed that behavioral adaptation was relatively easy and even enjoyable.

Physiological Adaptation to Weightlessness

Adaptation to weightlessness by U.S. Astronauts is well-documented, and research continues. A study of individual differences in adaptability to weightlessness by NASA physiologist Dr. Arnauld Nicogossian concludes that "Despite...numerous physiological shifts, humans appear to acclimate quite well to environmental variations", "there is wide variability in individual tolerances" and "the amount of time necessary for readaptation...exhibit large individual differences" (Nicogossian:135-136). This paper is concerned with skeletal adaptation as evidenced in changes to bone density, urine and fecal calcium levels, height, body fluid change, and blood serum hormones. Other physiological changes are interesting in that they support a thesis of a high adaptability of human biology, and a range of adaptability within a population. The summary information related to bone homeostasis that follows should not be considered complete.

The skeleton increases overall height by 3-6cm. The change in height of astronauts is temporary and returns to normal within one day. It appears to be the result of a straightening of the thoraco-lumbar curve of the spine in conjunction with an expansion of the interverteral discs as a result of unloading and fluid accumulation (Van Huss:19).

Calcium in the urine increases immediately and continues to increase for 30 days when it levels off. Calcium in the feces initially decreases but reverses after 10 days and continues to increase. Homeostasis is lost after 10 days and calcium loss has been measured to be as high as 300mg per day after 80 days on Skylab 4. Calcium homeostasis is restored after 30 days postflight but some bone loss is irreversible (Nicogossian:128-137; Collins:188-190; Holick:162).

Bone density decreases by approximately 0.5% per month. Radiographic examination of the distal right radius and ulna of Skylab participants showed no bone density loss to the arms (Holick:159; Van Huss:26). Similar examination of the central left calcaneus of Skylab 4 participants observed bone loss of approximately 4% (Nicogossian:204). The loss of heel bone would account for a 100mg per day. Since no loss in the arms is observed, it appears that other weight bearing bones in the lower skeleton are experiencing similar losses. Since the functional difference between the lower and the rest of the skeleton is support against gravity, the skeletal unloading in weightlessness seems to be a factor in bone loss.

Skeletal unloading reduces the electrical signal for bone formation. But blood serum calcium level is not initially excessive so the parathyroid does not immediately decrease PTH to reduce osteoclast activity. Bone demineralization continues at a normal rate causing an increased calcium serum level, which is sensed by the parathyroid. PTH is decreased which increases renal calcium elimination and decreases the hormonal D_3 secreted by the kidneys. Decreased calcium absorption in the small intestines and an increased elimination of calcium in feces results (Holick:165).

It is not known why this imbalance is not corrected but current theory centers on insufficient bone production caused by an uncoupling of the response mechanism of the hypothalamo-pituitary-adrenal response system (Vernikos-Danellis:7-8). Insufficient GH production from the pituitary would result in decreased cartilage cell production and decreased bone growth. While not conclusive, a post-flight increase in GH tends to support this theory. PTH production appears to be unaffected since osteoclast production is evidenced by bone demineralization. Similar but not as dramatic results are measured in bed-rest studies that simulate weightlessness (Holick:162).

Discussion

Evidence of human exposure to weightlessness confirms that human physiology is adaptable to a change in gravitational force, and demonstrates human flexibility in using a variety of locomotions. The effects of loading on bone growth is demonstrated and can account for the adaptation of the human skeleton to bipedalism. Dr. Hordinsky, the crew surgeon for Skylab 4 observed that "You throw someone in a new environment, and he's apt to have a tough time at first; but if he survives, he will tolerate it, and then begin to improve" (Cooper:181).

The Skylab missions and other biomedical experiments in weightlessness demonstrate the variability of human adaptability. Evolution requires variability for natural selection choices. With regard to bipedalism, adaptability meant survival. Being able to adapt to bipedalism meant increased ability to travel efficiently to gather food. This could have been a decisive factor for survival during times of decreased resources and increased competition. Survivability inherently implies the increased ability to provide genetic contributions, but bipedalism increased the advantage. Being able to travel efficiently meant being able to keep up with a troop and so have increased access for mating. Alternately, bipedalism afforded increased ability to cover territory and visit a larger population of potential mating partners.

It can be argued that results of biomedical experiments in weightlessness demonstrate the opposite, that adaptation to space is not complete and bone loss of the magnitude experienced in Skylab would not be survivable for greater than three years. While true, natural selection does not currently occur in weightlessness and so humans can only adapt and not evolve in weightlessness. It is interesting to note that while the evolution of highly sensitive systems such as blood homeostasis served hominids well in evolving to *H. sapiens*, these traits are a hindrance in adapting to extreme environments such as weightlessness. The ability to adapt, and not the individual adaptations, might be the most important evolutionary factor.

Humans adapt in response to a changing environment; essential to human origin is primate adaptability. Human adaptation to bipedalism demonstrates flexibility and provided efficiency in locomotion. It is the human condition to take risks for survival; the hominids who survived took the risks to leave the safety of the trees. Adaptation to an enviornment that provided an opportunity for disperment was fortunate. The combination of taking risks and adapting provided the means for *Homo* to survive, disperse, and inhabit almost the entire Earth. It seems to be inherently and essentially human to explore.

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